STUDIES IN THE LIFE-HISTORIES OF AUSTRALIAN ODONATA.

Part ii. Life-History of *DIPHLEBIA LESTOIDES* Selys.

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(Plate xxxiii.).

The beautiful dragonfly which is the subject of this paper, is the only representative of the family *Calopterygidæ* found in the temperate parts of Australia. In tropical Queensland a closely allied species, *D. euphœoïdes* Tillyard, is found. These two species are the only known members of a peculiar and isolated genus, whose nearest allies must be sought for amongst the numerous Malayan representatives of the family.

Comparatively, very little appears to be known of the early stages of the *Calopterygidæ*. The great majority of the species are found only in the Tropics, and there seems to be nobody available who can spare the large amount of time and trouble required to study them in their native haunts. The life-histories of various species of *Calopteryx* and *Hetærina*, however, which inhabit Europe and North America, have been thoroughly worked out, and at least one remarkable nymph of a tropical genus (*Euphœa*) appears to have been studied. The latter is, I believe, unique, amongst Odonate nymphs, in possessing paired gill-filaments along the sides of the abdomen, similar structures being commonly found in the nymphs of *Ephemeridæ*. It was, therefore, apparent that much new and interesting information might be expected from the discovery of the nymph of *Diphlebia*. Whether it would shew similarity of form or structure to *Calopteryx*, or whether it might not even possess some remarkable structure peculiar to itself, as in the case of *Euphœa*, were questions on which I was eager to throw some light; so that it was with more

than usual keenness and pleasure that I set about finding an answer to them.

Curiously enough, my first experience with a Diphlebia was the discovery of a new species, *D. euphœöides*, at Kuranda in North Queensland, in December, 1904. It was not until a year afterwards, when I visited the Mount Kosciusko district, N.S.W., that I came across the more widely distributed *D. lestoïdes*. On the Snowy River it was by no means uncommon, and was often a conspicuously beautiful object, as it rested, with expanded wings and brilliant blue body, on some rock in midstream, or on a twig of some overhanging bush. I was, however, quite unable to find out much about its habits. The males were rather shy, and difficult to capture; while the females were very seldom seen. Occasionally a pair were seen flying together over the water, but they were always attacked sooner or later by extra males, who generally succeeded in separating them or driving them off the river into the bush. Once or twice I came upon a pair at rest on a branch of a tree or bush, some distance from the water. We may reasonably conclude that the fertilisation of the ova is, therefore, generally accomplished away from the water, in some secluded spot of this kind. The next point to be observed was whether the male returned with the female to the river, and accompanied her during oviposition. Here I was completely at fault, for I never once saw a female ovipositing, although I was continually watching for them.

In pairing, the male uses his forcipate superior appendages to clasp the female round the prothorax, exactly as in the genus *Lestes*; the short inferior appendages press upon the occiput of the female.

I next saw this insect on the Goulburn River at Alexandra, Victoria, in December, 1906, but it was so extremely rare that I was unable to make any observations on it. In October, 1907, I was delighted to find it much nearer home, on the Woronora River, about twenty miles south of Sydney. Here I tried dredging and sweeping the water-weed with a net, but I failed to get any larvæ that could possibly be referred to this species. Nor was I able to discover any females in the act of ovipositing.

During September and October, 1908, I again visited the Woronora River, mainly with the idea of discovering something about *Diphlebia*. This year I failed to find it in its original locality, and was compelled to search out new haunts for it. On September 26th, I abandoned the main river, and tried the Heathcote Creek, a tributary, more accessible by rail, and not so rough for exploration. Some distance up this creek, the water comes down over a series of rocky ledges, forming small cascades and rapids. I was now using waders, and worked up the stream, dredging with the net under banks and along sandy bottoms, or in fact anywhere where larvæ might be found. While working under the roots of some "coral-fern" overhanging the creek, I obtained a most peculiar cast-skin of an Odonate nymph. It had been soaked in the water until it was soft and flabby, the only portions remaining at all intact being the head, and an enormous flat labium. My first impression was that it was the semifinal cast of some rare *Æschnid*, possibly *Telephlebia godeffroyi* Selys. However, the labium was of a peculiar type; the second joint of the antennæ was very long, and the anal opening of the abdomen very large and ragged, suggesting the possibility of some peculiar appendages. I had hopes that I was at last on the track of *Diphlebia*, and redoubled my efforts.

I again visited the same locality on October 3rd, but after dredging carefully all day, I met with no success. I now began to suspect that the larva might be an active creature inhabiting the bare submerged rocks, and that no amount of dredging would ever capture it.

The next Saturday, October 10th, I changed my tactics, and worked up the stream without using the net, peering carefully into the bright clear water, examining minutely the sides of the rocks, and the shady nooks under overgrown banks. Still no success! I sat down by the side of the stream to think it over, and was gazing abstractedly at a small clear runnel of water between two ledges of rock, when I suddenly came on the solution of the problem. There, on the broad green blades of a large water-reed, at a depth of a foot below the surface of the running

water, were two females of Diphlebia ovipositing. I watched the operation with the greatest interest. Kneeling down on the rock, and shading the reed from the sun with my hat, I was able to place my eye just above the insects. They appeared to be encased, as it were, in silver from head to tip, owing to the fact that they were completely surrounded with air. The operation of ovipositing was conducted fairly quickly, by raising the abdomen slightly, puncturing the reed with the ovipositor, and inserting an egg. Each female made two or three punctures nearly in a horizontal line; then, by contracting her abdomen, three or four more about one-quarter of an inch above the others, and so on; every now and then climbing higher up the reed. One female was working on one side of the reed, the other on the other; and one was about four inches above the other. I watched them for about five minutes, during which time they must have laid close on fifty eggs apiece. Then the upper female began to ascend the reed rapidly, and crawled out on to my hand, *perfectly dry*, the second one following half-a-minute later. I captured both and papered them. At the time I was astounded at the apparently large amount of air held by them under water, but a little reflection made me see how easily they contrived to do so. The long thin wings, folded back along the abdomen, reach nearly to its tip, and were so placed as to enclose between them a large amount of air, which passed also beneath the abdomen, forming a perfect sheath or covering. Between the head and prothorax also, on each side, a large bubble of air was held, and this extended backwards along the thorax and forwards under the eyes, so that practically the whole insect was protected from the water. Probably also the amount of air was sufficient to make the specific gravity of the insect about the same as that of water, and hence to enable it to move up and down in the swiftly running water with great facility.

I carefully gathered the reed, and carried it home in water for examination. I found each leaf full of punctures for a distance of about four to six inches. Each puncture contained beneath it a transparent egg about 1 mm. long. I cut off one portion of the

reed, about three inches, which was full of eggs, and placed it in clear water in a flat Petri dish; all the rest were put into a large jar of water.

The ovum is elongate-oval in shape, with one end rounded and the other pointed; the portion towards the pointed end is the thicker. *In situ*, the rounded end is furthest from the puncture, the point of the egg just resting in the opening. The ova do not darken materially during the first fortnight. At the end of three weeks they are dull yellowish. On November 15th, five weeks after they were laid, I examined the eggs in the Petri dish, and found them a pale rich brown in colour, with two minute black spots indicating the position of the eyes of the embryo. (See Plate xxxiii., fig. 3; *a*, ovum during first fortnight; *b*, same, five weeks old). Meanwhile the reed in the large jar had decomposed, and the ova were affected with fungus, so that I was obliged to throw them away.

On November 20th, forty-one days after the ova were laid, the first larva hatched in the dish. During the next few days more than a dozen hatched out; the rest apparently were either sterile or affected with some parasite which I was unable to determine; at any rate they failed to hatch out.

The young larva sits on the sharp edge of the reed. It is perfectly transparent, except for the two tiny black eyes. Length 1·5 mm over all; caudal gills long and slender, hairy; legs rather long. The creature is very active, and shows vigorous fight when poked at with a pin.

When about four days old the larva is 2 mm. long over all, and is brownish, slightly mottled, and considerably stouter in build than when first hatched. The colour darkens gradually until the first ecdysis takes place, after which it becomes pale and transparent again.

When the larvæ were about a month old, I removed one to a watch-glass in order to sketch it. It was most active, and I was unable to use the camera lucida. However, I made a careful pen-and-ink sketch of it, which is now reproduced in Plate xxxiii., fig. 4. Length over all 3 mm, colour pale straw; head round,

hairy in front, antennæ with seven joints approximately equal; all tibiæ with a few long hairs. Caudal gills distinctly triquetral, strong, transparent, very hairy.

I then introduced some animalcula into the watch-glass, and was fortunate in seeing the little larva feed. On the approach of a rotifer, the larva sat up in a pugnacious attitude, suddenly darted forward, seized the rotifer in its labium with a stroke as quick as lightning, and then shook and worried it from side to side with tremendous energy. The labium is very large for the size of the insect, and exceedingly powerful. After worrying its prey for a full minute or more, the larva retracted its labium, and appeared to hold the rotifer in it quite easily when closed, while it made its meal. I had further opportunities of watching these small larvæ feed when more fully grown, and in every case they seized their food in a most active manner, using their powerful legs to spring forward and asisst the labium to reach its prey.

On December 19th, 1908, prior to leaving Sydney for a few weeks, I emptied the Petri dish, containing about a dozen small larvæ, into a large cylindrical jar in which water-weed was growing, and having a clean shell-grit bottom. I then introduced a supply of infusoria sufficient to last until my return, and arranged to have the water kept up to a certain level, evaporation being very rapid in the hot summer months.

On my return, on January 27th, 1909, I immediately examined the jar. Apparently there was only one larva living, a robust fellow, skulking at the base of a twig, and so shy that, whenever I approached, he moved rapidly round to the other side of the twig, like an iguana. Length about 6 mm. over all; colour pale dirty white, touched with brown. It is difficult to say whether another ecdysis had taken place or not. About February 1st, the larva forsook its position on the twig, and hid itself under a large shell, where it remained for a week. On February 9th, I noticed a fine floating skin, showing that an ecdysis had taken place. Meanwhile the larva had returned to its position at the base of the twig, and appeared to be very alert and feeding well.

Towards the end of March, I carefully examined the larva and made a sketch of it. Length over all 8·5 mm., of which the caudal gills account for about 3 mm.; colour pale straw. *Head* rather square in front, with labium projecting slightly beyond it like a flat shelf. *Antennæ* seven-jointed, with the second joint elongated, the others shorter and about equal in length, except the top joint which is very thin and short; basal joint thickened; bases of joints 3-6 white, rest dark; second joint with small hairs all along it; a small tuft of two or three hairs at distal end of joints 3-6 (see Plate xxxiii., fig.5). *Eyes* black, with stiff hairs just below them. *Prothorax* and *forelegs* very strong and well developed, smooth. *Meso-* and *metathorax* together not much larger than prothorax; middle and hind legs fairly long, smooth. *Abdomen* rather short, thick, segments all very short; segment 10 fairly wide. *Caudal gills* 3 mm.; the lateral ones thick at bases, strongly triquetral, the cross-section apparently a triangle with base nearly flat and slant sides *convex* rather than concave; median gill less triquetral, narrower at base, projecting in a vertical plane at an angle of nearly 60° above the other two, which diverge in a horizontal plane at about the same angle. Under a lens the two main tracheæ can be seen branching out from the base of each gill, but these become transparent and soon divide up into innumerable smaller tracheæ which are practically invisible. For the first half of their length the gills increase in width, the top edge being convex, especially in the median gill; they then narrow rapidly to a long thin point, the last two-fifths being very hairy.

Towards the middle of April the nymph forsook its perch on the twig and hid under a shell, preparatory to another ecdysis. Soon afterwards it returned to the twig for a short time, and appeared very restless. I judged from its dark colour that the ecdysis was not yet over. During the next few days it became very sluggish, but fortunately it took up a position between a white shell and the glass of the jar, where I could watch it easily. On April 3rd, I noticed several water-fleas clustering round it, and on examination I found that it was dead, having only

partially succeeded in casting its old skin. The small water-fleas, too, had apparently partly destroyed its caudal gills, so that I was glad I had already made a sketch of them. Considering how very different both the food and the habitat of my artificially raised nymph were from those it would have had in a state of nature, it was scarcely to be expected that I could obtain a full-fed specimen. Possibly a diet of infusoria and small water-fleas may have been the cause, in the end, of its failure to undergo ecdysis; or living in stagnant water instead of a swift mountain stream may have been sufficient to prevent the full use of its strong muscular limbs, and so weakened it physically. I was fortunate, indeed, in keeping it so long alive and in being able to sketch the caudal gills and antennæ of the young larva.

To complete the life-history, it was necessary to find either the full-grown larvæ or the exuviæ. I doubt if it is possible ever to obtain the first, for I judge from my observations of the young larva that it probably lives in the crevices of the solid bed-rock of the stream, and is active enough to retreat rapidly away from any net or instrument used to snare it. Of the exuviæ I was fortunate enough in obtaining *four*, as the result of examining, for a whole day, rocks and boulders in the bed of the stream in the Rodriguez Pass, Blackheath, N.S.W., on November 7th, 1908. I found them clinging to the rock-surface, in company with a large number of ephemerid exuviæ of smaller size. The claws of the tarsi had such a firm hold of the rock that it was with the greatest difficulty that they could be detached without damage. I recognised these exuviæ at once as being similar to that found at Heathcote. Two of them also possessed shrivelled remains of caudal gills. An examination of antennæ and labium showed that they were the same species as the small larvæ bred from the Heathcote ova; in fact the latter, even in that early stage, showed a very close resemblance to the exuviæ in general form. As *Diphlebia lestoïdes* was the only zygopterous dragon-fly to be found along the Rodriguez Pass, where it is fairly common, I now felt quite certain that I had the exuviæ of that species, a full description of which I append.

Total length (excluding gills) 23·5 mm. *Head* large, 5·5 mm. wide, rather flat, slightly convex above; *eyes* not prominent, but well inset, the postocular lobes large, smooth, rounded; just under the eyes, in front, is a series of sharp curved spines, four in number, of which the front one is thick and strong; there is also a set of smaller spines near base of antennæ. *Antennæ* very long, 7 mm., smooth, thin, filiform, *second* joint very long. (Notice that the hairs on the antennæ of the young larva are absent in the exuviæ). *Ocelli* small, reniform, inconspicuous, placed in a triangle between the eyes. *Labium* enormous, measuring 6·2 mm. by 4·8 mm. when folded; perfectly flat underneath and projecting in front somewhat beyond the upper parts of the head, and backwards well past the procoxæ, so as to cover most of the underside of the prothorax; *mentum* rather shield-shaped, furnished with a set of small stiff spines on each side, and projecting slightly forward in front in a rounded curve with slight median indentation; no setæ present; *lateral lobes* strong, rather narrow, with several small spines on the outside along the basal portion; terminating in a sharp slender *movable hook* and in three smaller fixed spines or hooks; of these the middle one is the largest, and below its base is a much smaller one; the third lies behind and between the movable hook and the larger fixed hook (see Plate xxxiii., fig. 2). *Prothorax* well developed, rounded above; procoxæ set well forward under the head; forelegs exceedingly strong and large, femora broad, smooth, and flattened; tibiæ straight, smooth, and narrow; tarsi short, three-jointed, ending in two strong claws. *Meso-* and *metathorax* almost as wide as head; smooth, strongly built but not large; middle- and hind-legs also strongly built, with flattened femora. In the position of rest, the fore-legs are projected well forward and pressed close to the rock; the labium also presses close to the rock; the femora of the middle-legs lie almost flat, but those of the hind-legs are held with the broad flat sides nearly vertical; the whole position suggests that the insect lies concealed by clinging flat against the rock, and is ready to spring forward at its prey at any moment. Measurements of femora, tibiæ and tarsi of

fore-, middle-, and hind-legs are—fore, 5, 5·5, 2·5 mm.; middle, 6, 6, 2·5 mm.; hind, 8, 6, 3·5 mm. *Wing-cases* narrow, about 7·5 mm. long, reaching to just beyond segment 3 of abdomen. *Abdomen* very short, 12 mm., first three segments wider and longer than the rest; rounded above, flat beneath; segments 5-9 of about equal length and width, segment 10 shorter but of same width. *Caudal gills* (shrivelled) 10 mm., blackish, the lateral ones showing thick triquetral bases.

[See Plate xxxiii., fig. 1. N.B.—The caudal gills, as sketched in the Plate and enclosed in a dotted square, are reconstructed from the sketch made of the gills of the four-months old larva, and must not be taken as absolutely accurate.]

The colour of the larva is apparently a uniform dull dark brown all over.

Date of emergence.—The eggs are laid in November, and there is no doubt, judging from the progress of the larva in captivity, that they are full-fed in a year. The perfect insect, in the Sydney district, begins to emerge during the last week of September, and continues coming out till the end of October. In the colder districts of Kosciusko and Victoria, newly emerged individuals may be found late in January, by which time the insect has completely disappeared again in the Sydney district.

Hab.—Fast mountain-streams in New South Wales and Victoria.

The perfect insect has been described by de Selys, and again by René Martin* from specimens taken by Capt. Billinghurst at Alexandra, Vic. In my paper on "New Australian Species of the Family *Calopterygidæ*"† I have compared it with *D. euphœoïdes* and have corrected some errors of description due to the fading and changing of the brilliant colours in dried specimens. I have never, in the Sydney or Kosciusko districts, noticed the large range of variation in size and colour noticed by Martin.

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* "Les Odonates du Continent Australien," Mem. Soc. Zool. de France, 1901, p.243.

† These Proceedings, 1907, p.398.

Note on oviposition.—The method of oviposition in the tissues of reeds under water is not the only way employed by the species. During a visit to Leura, on December 5th, 1908, I distinctly saw a female alight on the almost vertical face of a mossy rock, over which the stream was trickling, and insert her ovipositor at least a dozen times into the moss-tissues. It then flew off up stream and repeated the operation further on.

In his work on the life-histories of American *Zygoptera*, Prof. J. B. Needham gives, for classification-purposes, the following differences between *Calopterygid* and *Agrionid* nymphs:—

"*Basal* segment of antennæ *very large*, as long as the other six together, median lobe of labium *with a very deep cleft*; gills thick, the lateral ones triquetral..... ....*Calopterygidæ*."

"Basal segments of antennæ *not* longer than succeeding segments; labium with a very shallow closed median cleft, or no cleft at all; gills thin, lamelliform..... .....*Agrionidæ*."

This classification was adopted on the knowledge afforded by the study of the nymphs of *Calopteryx* and *Hetærina* only. It will be seen at once that the nymph of *Diphlebia* differs in important respects from those of these two genera.

Firstly, as regards the antennæ. In *Diphlebia*, it is the *second* joint which is greatly elongated, the basal joint being short and thick. The elongation of this joint, however, is not so great as that of the basal joint of *Calopteryx*. I am inclined to regard elongated antennæ in dragonfly nymphs as a primitive character. The reduction in length has been carried to a great extreme in the imagines, and one can see no reason at all, even in the nymphal stages, for the continuance of elongated antennæ. In all burrowing nymphs they have become very short, and in the *Gomphinæ* the number of joints is actually reduced to four. The possession of long antennæ may then merely mark out the more primitive families, but it will also mark isolated groups which may have been placed outside of these families for more important structural reasons. I shall show, in a later part of this paper, that the long basal joint is possessed by *at least one Agrionid* found commonly in parts of Australia. This suggests that it

was a characteristic of the original *Zygopterid* stock before the differentiation of the *Agrionidæ* from the *Calopterygidæ* was fully established.

Secondly, as regards the labium. Unlike the labia of *Calopteryx* and *Hetærina*, that of *Diphlebia* is *not* deeply cleft medially; in fact it possesses a median lobe of the usual *Agrionid* form. Apart from this, the labium of *Diphlebia* is remarkable (*a*) for its great size; (*b*) for the broad shield-shaped mentum, recalling that of the *Æschnidæ*; (*c*) for its flatness, which also recalls that of the *Æschnidæ*. There is, however, a considerable resemblance in the form of the *lateral* lobes in *Diphlebia* and *Calopteryx*; each carrying, besides the movable hooks, *three* fixed hooks or teeth. *Hetærina* appears to possess *four* fixed teeth, but the dentition in this genus really consists of two parts, the upper one being itself tridentate. Both lateral and mental setæ appear to be present in *Hetærina* and *Calopteryx*, though in the latter genus they are nearly reduced to vanishing point. *No setæ* are present in *Diphlebia*.

Thirdly, as regards the caudal gills. Here the triquetral character is even more pronounced in *Diphlebia* than in *Calopteryx*; for even the median gill of *Diphlebia* is distinctly triquetral and not lamelliform, though this gill is distinctly flatter and more leaf-like than the lateral ones. It is a pity that a full-grown *Diphlebia* nymph with perfect gills cannot be obtained, for it must be understood that those sketched in the central figure of the plate are, at best, approximate only, being drawn, without actual measurements, from a sketch of a four-months-old larva. It will be seen that in the young larva the gills were hairy all over, but that, at four months, the hairs are restricted to the outer two-fifths. Hence it is quite possible that when the final nymphal stage is reached they may be completely hairless. I am unable to find hairs on the shrivelled remains of the gills attached to the exuviæ, but their condition is not such as to warrant the deduction that they may not have been there originally.

In these large triquetral gills we have clearly a form handed down from remote antiquity. If the presence of numerous

branched tracheæ in these gills suggests anything at all, it must be that *originally* they were in some way organs of respiration. In the *Agrionidæ* we see them converted from their original use into practically an aid to locomotion only. It is certain that the loss of these gills, even in *Diphlebia*, does not affect the respiration of the insect in any way, for two of the four exuviæ I possess *have no gills left at all.* I noticed several of my young larvæ without caudal gills only a few days after birth, so that it is clear that they are easily broken off and lost. After an ecdysis they are again replaced, though usually somewhat smaller than a gill that has not been lost previously. The triquetral form suggests a modification of some original structure capable of receiving a large quantity of water for purposes of respiration. I doubt whether even the wide lateral gills of *Diphlebia*, fed by two large tracheæ, are of any use at present for auxiliary respiration. The form of structure has probably persisted long after its use has vanished. Be that as it may, the triquetral gill appears to be at present confined to the *Calopterygidæ* alone.

The larva of *Diphlebia* shows no signs of the paired abdominal gill-structures found in *Euphœa*. Such structures could scarcely be expected to persist in what, I think, must be regarded as a highly successful and specialised branch of the Calopterygid stock. In the imago, the reduction of cross-veins in the wings has been carried out to such an extent as almost to have reached the end achieved by the *Agrionidæ*. One feels that there is much to ponder over in the unerring insight which led de Selys to give the name *lestoïdes* to this peculiar insect. There is more than a superficial resemblance, especially if the comparison be made, not with *Lestes* but with *Argiolestes*. Though more than two antenodals still persist, only the first two are continuous into the subcostal region; so that the elimination of the other three or four is at least half-accomplished. In the larva itself we probably have the secret of the success of this type. Its whole form,—the enormous strength of the legs, the huge labium and in-set eyes—shows us at once that Nature has evolved a successful type capable of holding its own against all its enemies,

and evolved it along a line entirely different from all other Australian *Zygoptera*, except perhaps *Argiolestes*. The larva is, in fact, an active predatory insect, and probably is quite able to defend itself against attacks by enemies larger than itself, using its labium as well to ward off attack as to capture its food, and its strong legs to enable it to retreat quickly backwards into a crevice if the necessity arises. I was much struck by the vigorous way in which the newly hatched larvæ shewed fight when attacked with a fine pin-point. They would back vigorously, darting out their labia with great rapidity, and finally, if pressed, dodge rapidly aside, all the time keeping ceaseless vigil. I have never been able to provoke any other Zygopterous larva to shew fight. In this respect, *Diphlebia* resembles some of the large *Æschnidæ*, whose larvæ, dwelling on submerged sticks and twigs, stalk their prey with great perseverance and watchfulness. Possibly this may suggest the reason for the convergence in the form of its labium to that of an Æschnid.

In conclusion, I regret that my attempt to raise this interesting larva has been only partially successful. Probably a closer approximation to natural conditions — running water, and animalcula obtained from its natural haunts—may be the road to final success.

EXPLANATION OF PLATE XXXIII.

Diphlebia lestoïdes.

Fig. 1.—Exuviæ (×4). N.B. The caudal gills, enclosed in a dotted square, are supplied from a sketch of those of a larva four months old; those of the exuviæ are shrivelled.

Fig. 2.—Labium.

Fig. 3.—Ova, *a*, one week old; *b*, five weeks old.

Fig. 4.—Larva one week old.

Fig. 5.—Antennæ of four-months-old larva.